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# Assessing Significance of Physiological Differences among Three Esocids with a Bioenergetics Model

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To predict stocking success of esocids in Ohio waters with different thermal regimes, we measured individual food consumption, conversion efficiency, growth, and metabolic rate for Ohio stocks of northern pike (*Esox lucius*), muskellunge (*E. masquinongy*), and their hybrid, tiger muskellunge, in laboratory experiments. The first three parameters were quantified during 2-wk experiments of ad libitum feeding on fathead minnows (*Pimephales promelas*) at seven constant temperatures (5, 15, 20, 22.5, 25, 27.5, and 30°C). The food consumption and growth data suggest that northern pike should grow faster than muskellunge at cool temperatures (≤20°C), but slower than muskellunge at warm temperatures (>25°C). Latitudinal differences in their natural distributions might explain this observation. Growth data of the hybrid showed no such obvious relationship to either of the parents. Metabolic rates were determined by measuring oxygen consumption in a closed, static respirometer at five constant temperatures (5, 15, 20, 25, and 30°C). We found little difference in metabolic rates among the three taxa. To examine these data further, we used a bioenergetics model that simulated different stocking conditions, both natural (thermal regime and prey availability) and human controlled (stocking size and date). With this model, we predicted growth for 12–15 mo after stocking. In general, summer-stocked fish were about 35–90% larger 15 mo after stocking than were fall-stocked fish 12 mo after stocking. More specifically, the combined effect of ration and temperature permitted hybrids to grow faster than the parents in all simulations. Northern pike grew larger than muskellunge in a cool system, but smaller than muskellunge in a warm system with summer stocking. Based on bioenergetic considerations, tiger muskellunge should outgrow both northern pike and muskellunge in thermal regimes common to Ohio waters.

Pour déterminer le succès de l'ensemencement d'esocidés dans des cours d'eau de différentes températures en Ohio, nous avons mesuré la consommation d'éléments nutritifs et leur transformation, le taux de croissance et le métabolisme du brochet (*Esox lucius*), du maskinongé (*E. masquinongy*) et de l'hybride résultant du croisement de ces deux espèces, en étudiant en laboratoire des sujets prélevés dans les stocks de l'Ohio. Nous avons quantifié les trois premiers paramètres mentionnés ci-dessus en étudiant pendant 2 sem des têtes-de-boules (*Pimephales promelas*) nourries à volonté et conservées à sept températures différentes (5, 15, 20, 22,5, 25, 27,5 et 30°C). D'après les résultats que nous avons obtenus sur la consommation de nourriture et la croissance, le brochet devrait se développer plus rapidement que le maskinongé en eau froide (≤20°C) et plus lentement en eau chaude (>25°C). Ce phénomène s'explique peut-être par la différence de latitude qu'il y a entre l'aire de distribution naturelle de ces deux espèces. Par ailleurs, les données que nous possédons sur la croissance de l'hybride ne révèlent aucune relation évidente avec l'un ou l'autre des parents. Nous avons évalué le métabolisme en mesurant la consommation d'oxygène dans un respiromètre statique fermé, à cinq températures différentes (5, 15, 20, 25 et 30°C) ; il y avait peu de différence entre les trois poissons. Pour pousser l'analyse, nous nous sommes servi d'un modèle représentant les processus bioénergétiques avec lequel nous avons simulé différentes conditions d'ensemencement mettant en jeu des facteurs naturels (température de l'eau et abondance des proies) et des éléments sous contrôle (nombre de poissons ensemencés et date de l'opération). Nous avons ainsi pu prévoir la croissance des poissons durant les 12 ou 15 mo suivant l'ensemencement. En général, les poissons ensemencés en été étaient de 35 à 90 % plus gros au bout de 15 mo que les poissons ensemencés en automne, au bout de 12 mo. Plus précisément, nous avons constaté qu'en raison de l'effet combiné de la ration et de la température, les hybrides se développent plus rapidement que les poissons parents, quelles

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que soient les conditions. Le brochet devient plus gros que le maskinongé en eau froide, mais il demeure plus petit en eau chaude lorsque l'ensemencement a lieu en été. D'après nos données sur les processus bioénergétiques, l'hybride devrait se développer mieux que ses parents à la température des eaux qu'on trouve généralement en Ohio.

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Northern pike (*Esox lucius*) and muskellunge (*E. masquinongy*) have been stocked beyond their natural ranges for nearly 100 yr to provide trophy fisheries across the United States (Webster et al. 1978). Within the last 20 yr the hybrid, tiger muskellunge (male northern pike × female muskellunge), also has been stocked into lakes and reservoirs. Hybrids have been chosen over their parents because of hatchery-related benefits (Hesser 1978); relative to their parents, hybrids exhibit (1) greater survival through hatching, (2) greater disease resistance, and (3) the ability to feed readily on dry food (a definite economic advantage). Though the hybrid has these rearing advantages, their survival after stocking has often been quite low (Stein et al. 1981). Thus, to decide which of these esocids should be stocked, information related to poststocking survival must be gathered for each taxon.

Previous comparative studies on thermal tolerance (Bonin and Spotilla 1978; Scott 1964), growth rates (Weithman and Anderson 1977), and conversion efficiencies of esocids in laboratory and pond experiments suggest that abiotic factors (particularly temperature) affect northern pike, muskellunge, and tiger muskellunge differently. In three small impoundments in West Virginia, Hess (1981) found that tiger muskellunge grew faster than muskellunge in one lake, muskellunge and northern pike grew similarly in a second, and all three taxa grew similarly in a third lake. These studies demonstrate how different situations might favor different taxa, but they do not provide the mechanisms for such; therefore, it is nearly impossible to predict which taxon would do best in a particular system.

The problem is twofold. First, a multiplicity of variables, most notably temperature and ration, interact to determine growth. Therefore, it is not always clear why a single taxon grows well (or poorly) in a given system. Second, the interaction of ration and temperature probably differs among the three taxa. An efficient means of examining this complex problem is mathematical modeling. Bioenergetics models that summarize the unique physiological responses of different fishes to ration and temperature allow investigators to take into account both the effects of ration and temperature on individual fishes and the differences between fishes. Bioenergetics models, as an aid to field research, previously have been used to examine growth of walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) (Kitchell et al. 1977), largemouth bass (*Micropterus salmoides*) (Cochran and Rice 1982; Rice et al. 1983), and sea lampreys (*Petromyzon marinus*) (Kitchell and Breck 1980). Determining system characteristics that favor each esocid is critical, because maintaining a tiger muskellunge stocking program also requires adult northern pike and muskellunge. However, investigators will not fully understand results from field experiments until some of the physiological factors that contribute to those results are defined and understood. Therefore, our first objective was to determine differences in metabolism, food consumption, conversion efficiency, and growth among northern pike, muskellunge, and tiger muskellunge as a function of temperature, and summarize these data in a bioenergetics model for each taxon. This approach uses a simple mass balance equation where caloric intake is equal to all energetic costs plus growth. Taxon-specific functions for food consumption and metabolism were incorporated into the model with the assumption that these experimental values approximated field values.

We expected to find physiological differences related to temperature between northern pike and muskellunge because of latitudinal differences in their natural distributions. Northern pike extend north to the Arctic Circle and south into central Ohio, whereas muskellunge extend north only to southern Canada and south to Tennessee (Crossman 1978). Although field data are available that compare hybrid growth with that of its parents, these data are only loosely connected with temperature. One hypothesis suggests that the hybrid reaction to a range of temperatures would be intermediate to both parents. Alternatively, hybrid vigor could permit tiger muskellunge to grow more efficiently than its parents (Scott 1964; Pecor 1978).

The second objective of this study was to use the bioenergetics model to assess the significance of differences among these three taxa as they relate to stocking options and thermal environments. When planning stocking strategies, managers might have data on the thermal regimes of lakes they wish to stock and might be flexible in choosing fish species, stocking size, and stocking date. By modelling growth of each esocid with different thermal regimes, stocking dates, and size at stocking, we can compare directly the success of each taxon in different environments.

## Materials and Methods

### Fish stocks

Young-of-year northern pike, muskellunge, and tiger muskellunge were obtained from Ohio Division of Wildlife fish farms at St. Marys, London, and Kincaid, respectively. The northern pike stock originated from Lake Erie and has been maintained in hatchery ponds at St. Marys (Auglaize County) since initial collection over 25 yr ago. The Ohio muskellunge stock originated from Ohio River tributaries in southern Ohio and has been maintained in Ohio reservoirs for over 25 yr. Muskellunge of the Ohio River drainage system are recognized as a subspecies, *E. m. ohioensis*, separate from more northern stocks (Trautman 1957). The tiger muskellunge used in these experiments were products of male northern pike (originally from St. Marys fish farm) collected from Lake Rupert (Vinton County) and female muskellunge collected from Rocky Fork Lake (Highland County). All three taxa were held in 400-L aquaria at 10–20°C until they were used in experiments.

### Metabolic Rate Experiments

Oxygen consumption, as a measurement of metabolic rate, was measured with a closed, static respirometer, which consisted of a round 4.68-L tank with a clear Plexiglas cover (sealed

with stopcock grease) and was immersed in a constant-temperature (5, 15, 20, 25, or 30°C) water bath. The oxygen probe from a Beckman model 0260 oxygen ($O_2$) analyzer fit through a hole in the Plexiglas; a magnetic stirrer on top of the chamber circulated water. Output from the oxygen analyzer was monitored continuously with a chart recorder. Records were digitized with a Hewlett-Packard model 9825B computer and a model 9874A digitizer to determine the initial and final dissolved oxygen (DO) content of the water, and then the amount of oxygen consumed per gram of fish per hour was determined. Rate of metabolism was derived from oxygen consumption by converting mg $O_2 \cdot g^{-1} \cdot h^{-1}$ to $g \cdot g^{-1} \cdot d^{-1}$ with an oxycalorific coefficient of 3.24 cal·mg $O_2^{-1}$ (Elliott and Davidson 1975) and a fish caloric value of 860 cal·$g^{-1}$ (R. Stein, unpubl. data) for use in the model.

Following the suggestions of Brett (1962), we allowed time for the fish to acclimate to temperature and recover from handling. Before experiments, fish were held at test temperatures with a photoperiod of 16 h light : 8 h dark for at least 1 wk (usually 2 wk) and were put in the respirometer 15 h before the experiment. Temperatures were changed slowly (1–3°·$d^{-1}$) when acclimating fish from holding temperature to test temperature. Fish were starved for at least 120, 72, and 24 h for experiments at 5, 15, and ≥20°C, respectively. These periods approximate time of gut evacuation, which we determined for tiger muskellunge at 5, 15, and 25°C (Bevelhimer 1983). At least 30 min before experiments began in the morning, the respirometer water was flushed (with minimal disturbance of the fish) to eliminate overnight accumulation of $CO_2$ or ammonia. Water in the respirometer was aerated continuously except during experiments. Amount of DO at the beginning of a trial depended on the test temperature and usually was between 7.0 and 10.0 mg·$L^{-1}$. Amount of DO at the end of a trial never fell below 5.0 mg·$L^{-1}$. At warm temperatures (>20°C), experiments lasted about 0.75 h, and at cool temperatures (<20°C) about 1–1.5 h was required for adequate measurements of oxygen consumption. At least 13 trials with at least four individuals were performed for each of the three taxa at each temperature. At the end of each experiment, fish were weighed and measured. Total lengths were 128–227 mm; weights were 9.5–53.2 g ($\bar{X}$ = 20.7 g).

To minimize activity, the stirrer was only turned on 5–10 min at the beginning and at the end of each trial to obtain initial and final DO. When the stirrer was off, which was a majority of the time, fish were usually inactive. When a fish was active, its movement tended to stir the water around the oxygen probe causing erratic output on the chart recorder, which could be examined later to determine if a fish had been active. Those trials in which fish were active more than 35% of the time (as determined by periodic observation and/or examination of the chart record) were not included in the analysis.

The metabolic rates determined in these experiments might be best designated as "low routine" metabolism or "uncontrolled standard" metabolism as defined by Beamish and Dickie (1967). Whatever the label, we feel that the respiration rates approximate the metabolism of inactive fish in the field. Costs of activity will be addressed later in the model section.

An equation that expresses respiration rates as an exponential function of weight, and includes the temperature dependence as a form of van't Hoff's $Q_{10}$ rule (Brett and Groves 1979), was determined for each of the three taxa and for all taxa combined:

$$(1) \quad \text{mg } O_2 \cdot g^{-1} \cdot h^{-1} = a_2 \cdot B^{b_2} \cdot e^{mT}$$

or, in linear form:

$$(2) \quad \ln(\text{mg } O_2 \cdot g^{-1} \cdot h^{-1}) = \ln(a_2) + b_2 \cdot \ln(B) + mT$$

where $a_2$ is an intercept constant, $b_2$ is the weight-dependent constant, $m$ is the temperature-dependent constant (related to $Q_{10}$ by $Q_{10} = e^{10 \cdot m}$), $B$ (biomass) is wet weight (grams), and $T$ is temperature (degrees Celcius). Because we used a narrow range of sizes (9–53 g), values for $b_2$ could not be determined accurately. Diana (1982) estimated $b_2$ at −0.18 with a larger size range (5–1200 g) of northern pike at 14°C. Because Beamish (1970) suggested that $b_2$ does not change with temperature, we used this value at all temperatures, making the additional assumption that it did not differ among the three taxa. To determine total respiration (mg $O_2 \cdot h^{-1}$), 0.82 ($b_2$ + 1) can be used for the weight coefficient. The constant values, $a_2$ and $m$, were determined with a least squares linear regression procedure, where ln (mg $O_2 \cdot g^{-1} \cdot h^{-1}$) − (−0.18·ln ($B$)) was the dependent variable, and $T$ was the independent variable. Duncan's multiple range test (Helwig and Council 1979) was performed on these data to determine if differences among taxa were substantial enough to warrant three separate equations.

## Food Consumption Experiments

Individual esocids at seven constant temperatures (5, 15, 20, 22.5, 25, 27.5, and 30°C) were fed ad libitum on live fathead minnows (*Pimephales promelas*) that were supplied daily for 14 d. Initial predator lengths were 125–210 mm; initial weights were 7.2–43.5 g ($\bar{X}$ = 19.3 g). Mean sample size was 15 individuals per taxon per temperature for experiments at temperatures ≤25°C and 9 individuals per taxon per temperature for experiments at temperatures >25°C. Laboratory aquaria (29–118 L) were divided so that two or three fish could be tested per tank. Minnow lengths were 25–40% the total length of fish to which they were fed, which corresponded to preferred sizes determined by Gillen et al. (1981). All minnows added to the tank and any dead ones removed were damp dried with a paper towel and weighed to determine the amount of food consumed. After 14 d, remaining minnows were removed, and the esocids were starved for 120, 72, or 24 h for experiments at 5, 15, and ≥20°C, respectively, before final weighing to insure that final weights represented actual growth and not an undigested meal (Bevelhimer 1983). Because prey were eaten every 3–6 d at 5°C instead of daily as at other temperatures, 5°C experiments ended when a fish consumed its first minnow after day 13. Remaining minnows were removed, and fish were starved for 120 h before final weighing. Thus, 5°C experiments ranged from 14 to 20 d, but bias (overestimated final weights) due to different amounts of food in the stomach was prevented.

Maximum consumption rate ($C_{max}$, g food consumed·g $fish^{-1} \cdot d^{-1}$), gross conversion efficiency (change in g wet weight·g food $consumed^{-1}$), and relative growth (change in g wet weight·g mean $weight^{-1} \cdot d^{-1}$) were calculated for each fish (note: mean weight is an arithmetic mean of initial and final weights). Energy content of the esocids and the fathead minnows did not differ; mean energy content of both was 860 cal·$g^{-1}$ (R. Stein, unpubl. data). Energy content of fishes does vary with season (Diana and Mackay 1979; Pierce et al. 1980), but sufficient data for juvenile esocids or fathead minnows were not available to quantify specific seasonal differences.

After trying different types of equations (i.e. second, third, fourth, and fifth order, and log–log and semi-log transformations), we decided that a third-order polynomial equation best

reflected the dependence of food consumption on weight and temperature:

$$(3) \quad C_{max}(g \cdot g^{-1} \cdot d^{-1}) = a_1 \cdot B^{b1} \cdot e^{(xT + yT^2 + zT^3)}$$

or, in linear form:

$$(4) \quad \ln C_{max} = \ln (a_1) + b_1 \cdot \ln (B) + xT + yT^2 + zT^3$$

where $a_1$ is an intercept constant, $x$, $y$, and $z$ are taxon-specific temperature-dependent constants, $b_1$ is a weight-dependent constant, $B$ is wet weight (grams), and $T$ is temperature (degrees Celcius). Because the literature contains no values of $b_1$ for esocids, and we could not accurately determine it with our data, we assumed that $b_1 = b_2 = -0.18$. Although Brett and Groves (1979) indicated no reason why $b_1$ should equal $b_2$, it was convenient for this study. This value provided food consumption rates for large fish (up to 1000 g) that we felt were realistic, based on growth of juvenile tiger muskellunge in a small impoundment (Stein et al. 1982). The taxon-specific constants ($a_1$, $x$, $y$, and $z$) were determined with a least squares linear regression procedure with $\ln (C_{max}) - (-0.18 \cdot \ln (B))$ as the dependent variable, and $T$, $T^2$, and $T^3$ as independent variables. Duncan's multiple range test was performed on these data to determine if differences among taxa were substantial enough to warrant three separate equations.

## Model

### Basic Components

Specific growth of juvenile esocids can be calculated with an equation similar to that used by Kitchell et al. (1977) for yellow perch:

$$(5) \quad G = C - (M + F + U)$$

where

$G$ = specific growth rate ($g \cdot g^{-1} \cdot d^{-1}$), C = specific rate of food consumption, $M$ = specific rate of metabolism, which includes inactive, active, and specific dynamic action (SDA) components, $F$ = specific rate of egestion, and $U$ = specific rate of excretion.

Each of the terms of this equation will be dealt with separately in the following descriptions.

*Consumption*

Specific rate of consumption was determined by the equation

$$(6) \quad C(g \cdot g^{-1} \cdot d^{-1}) = C_{max} \cdot P$$

where $C_{max}$ (eq. 3) is the maximum rate at a particular temperature for each taxa, and $P$ is a proportional constant indicating the proportion of $C_{max}$ actually consumed.

*Metabolism*

The total cost of metabolism includes the increase above standard metabolism due to increased activity and the cost of processing and assimilating food. The following factors were incorporated with the basic metabolic rate equation (eq. 1) to determine the additional cost of activity: direct relationship of swimming speed to increase in oxygen consumption (Wohlschlag and Juliano 1959; Brett 1965); burst-speed swimming (Webb 1977); cruise-speed swimming (Diana 1980); amount of daily activity at cruising speed (Diana 1980); the daily duration of burst-speed swimming based on duration of burst-speed swimming per feeding bout (Moody et al. 1983); and the number of feeding bouts per day (Bevelhimer 1983). The first factor, the relation of swimming speed to increased oxygen consumption, has not been computed for esocids, so this could be a source of error. Throughout these computations, we assumed that the three taxa did not differ in activity or swimming speeds. With activity durations and swimming speeds constant across size, temperature, and taxon, the inclusion of the activity factor increases the metabolic rate by 13% over the standard metabolic rate. For a more detailed explanation, see Bevelhimer (1983).

The cost of processing and assimilating food (specific dynamic action (SDA)) was assumed to be a constant proportion ($S$) of food consumption ($C$).

$$(7) \quad SDA(g \cdot g^{-1} \cdot d^{-1}) = S \cdot C.$$

Jobling (1981) suggested that $S$ varies with ration (quality and quantity) and temperature; however, for the sake of simplicity and the lack of specific values for esocids, we chose to use an average value suggested by Brett and Groves (1979) for all fishes, $S = 0.14$. Therefore, the total metabolic cost can be determined by the following equation:

$$(8) \quad M(g \cdot g^{-1} \cdot d^{-1}) = 1.13 \cdot (a_2 \cdot B^{b_2} \cdot e^{mT}) + 0.14 \cdot C.$$

For use in the bioenergetics model, the intercept value $a_2$ was converted from mg $O_2 \cdot g^{-1} \cdot h^{-1}$ to $g \cdot g^{-1} \cdot d^{-1}$ by multiplying $a_2 \cdot (3.24 \text{ cal} \cdot \text{mg } O_2^{-1}) \cdot (1 \text{ g} \cdot 860 \text{ cal}^{-1}) \cdot (24 \text{ h} \cdot d^{-1})$.

*Egestion and excretion*

Energy losses from egestion ($F$, feces) and excretion ($U$, urea and other nitrogenous wastes) were assumed to be constant proportions of consumption ($C$) expressed by the equations

$$(9) \quad F(g \cdot g^{-1} \cdot d^{-1}) = f \cdot C,$$

where $f$ is the proportion of food consumed that is egested and

$$(10) \quad U(g \cdot g^{-1} \cdot d^{-1}) = u \cdot C,$$

where $u$ is the proportion of food consumed that is excreted.

No data were available for egestion ($f$) or excretion ($u$) for esocids; hence, we chose to use constant values of $f$ (0.20) and $u$ (0.07) as suggested by Brett and Groves (1979), who averaged values from a variety of fishes. Egestion and excretion rates may vary substantially with ration and temperature (Elliott 1976), but the combination of decreasing egestion losses and increasing excretion losses with increasing temperature produces a combined effect that varies little across temperature (Kitchell et al. 1977). Symbols and values of all model parameters discussed in this section are summarized in Table 1.

### Variable Components

The model includes variables that were useful in simulating different stocking options, such as time of stocking, fish size at stocking, and choice of lakes (differing in thermal regime). We chose two stocking dates, one in summer and one in fall, that were typical of actual stocking dates in Ohio: day 180 (June 29) and day 270 (September 27). All simulations ended on September 27 of the second year; thus, simulations of summer stocking ran 15 mo whereas those for fall ran 12 mo. Typical sizes at the stocking dates were 9 g (125 mm) in summer and 80 g (250 mm) in fall, though fall sizes can be manipulated by hatchery managers to produce fish smaller or larger than 80 g.

Two annual thermal regimes were incorporated in the model to evaluate the importance of temperature on growth. Temperatures from 1 m deep at Caesar Creek Lake (1980) in southwestern Ohio represented a thermal regime typical of Ohio

TABLE 1. Symbols, definitions, and parameter values used for simulating growth of northern pike (NP), muskellunge (M), and tiger muskellunge (TM).

| Equation | Symbol | | Parameter description | Value | Standard error | Source[a] |
|---|---|---|---|---|---|---|
| Metabolism | | | | | | |
| 1 | $a_2$ | | Intercept coefficient | 0.1025 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ or $9.27 \times 10^{-3}$ $g \cdot g^{-1} \cdot d^{-1}$ | +0.0062, −0.0059[b] $+0.56 \times 10^{-3}$, $-0.54 \times 10^{-3}$[b] | 3 |
| 1 | $b_2$ | | Weight-dependent exponent | −0.18 | ±0.05[c] | 2 |
| 1 | $m$ | | Temperature-dependent exponent | 0.055 | ±0.003 | 3 |
| 10 | $S$ | | Specific dynamic action factor | 0.14 | | 1 |
| Food consumption | | | | | | |
| 3 | $a_1$ | (NP) | Intercept coefficient | $2.44 \times 10^{-2}$ $g \cdot g^{-1} \cdot d^{-1}$ | $+0.81 \times 10^{-2}$, $-0.61 \times 10^{-2}$[b] | 3 |
| | | (M) | Intercept coefficient | $1.26 \times 10^{-2}$ $g \cdot g^{-1} \cdot d^{-1}$ | $+0.32 \times 10^{-2}$, $-0.25 \times 10^{-2}$[b] | |
| | | (TM) | Intercept coefficient | $4.60 \times 10^{-3}$ $g \cdot g^{-1} \cdot d^{-1}$ | $+1.29 \times 10^{-3}$, $-1.01 \times 10^{-3}$[b] | |
| 3 | $b_1$ | | Weight-dependent exponent | −0.18 | | 3 |
| 3 | $x$ | (NP) | Temperature-dependent exponent | −0.024 | ±0.070 | 3 |
| | | (M) | Temperature-dependent exponent | 0.060 | ±0.057 | |
| | | (TM) | Temperature-dependent exponent | 0.401 | ±0.060 | |
| 3 | $y$ | (NP) | Temperature-dependent exponent | $1.25 \times 10^{-2}$ | $\pm 0.45 \times 10^{-2}$ | 3 |
| | | (M) | Temperature-dependent exponent | $0.75 \times 10^{-2}$ | $\pm 0.37 \times 10^{-2}$ | |
| | | (TM) | Temperature-dependent exponent | $-1.40 \times 10^{-2}$ | $\pm 0.38 \times 10^{-2}$ | |
| 3 | $z$ | (NP) | Temperature-dependent exponent | $-3.26 \times 10^{-4}$ | $\pm 0.86 \times 10^{-4}$ | 3 |
| | | (M) | Temperature-dependent exponent | $-2.16 \times 10^{-4}$ | $\pm 0.69 \times 10^{-4}$ | |
| | | (TM) | Temperature-dependent exponent | $1.55 \times 10^{-4}$ | $\pm 0.72 \times 10^{-4}$ | |
| 11 | $f$ | | Egestion factor | 0.20 | | 1 |
| 12 | $u$ | | Excretion factor | 0.07 | | 1 |

[a]Parameter sources: 1, Brett and Groves (1979); 2, Diana (1982); 3, derived in this study.
[b]Plus and minus errors differ because this coefficient was determined with logarithmic transformation.
[c]95% confidence limits (Diana 1982).

impoundments. Water temperatures were not measured during the winter at Caesar Creek Lake, so we assumed the temperature was 2°C when the lake was ice-covered. For a contrasting temperature regime, we obtained daily temperatures from 6–7 m deep at Alum Creek Lake (1981) in central Ohio. Although oxygen is usually available at 6–7 m deep in Alum Creek Lake, this condition is atypical of Ohio impoundments during summer. However, this thermal regime will be useful for examining the response of the three esocids to different annual temperature regimes (henceforth known as warm, Caesar Creek Lake and cool, Alum Creek Lake, illustrated in Fig. 1).

Evidence from radio telemetry studies (Headrick et al. 1982) suggests that northern pike regulate their body temperatures by moving to those available water temperatures that are more conducive to efficient growth. We simulated the effects of behavioral thermoregulation by permitting each esocid to seek its optimal temperature for growth (as determined in growth simulations at constant temperatures and maximum ration) whenever water temperatures rose above optimal. The warm regime from Caesar Creek Lake was used for these simulations. Temperature could be reduced no more than 4°C, hypothetically, the maximum allowable change in Caesar Creek Lake due to the presence of a thermocline, below which was an anoxic hypolimnion.

We also manipulated ration level (controlled by the value of $P$) to reflect prey availability and seasonal food requirements. Constant levels were established through iteration with the bioenergetics model to produce target weights on December 31 (first year's end) and September 27 (end of simulation) by adjusting the value of $P$. Target weights of 300 g by December 31 and 900 g by September 27 were estimated from average sizes of YOY (about 375 mm) and yearling (about 525 mm) esocids from West Virginia lakes (Hess 1981). Ninety percent of $C_{max}$ ($P = 0.9$) was required to reach target weight by December 31. From January 1 to September 27, 55% of $C_{max}$ ($P = 0.55$) produced average weights of about 900 g.

Based on the constant $P$ values mentioned above and seasonal prey densities from field sampling (Stein et al. 1982), we developed a hypothetical, variable ration scheme to examine the effect of variable ration on seasonal growth. These rations were estimated for immature fish and would probably be inappropriate for adult fish experiencing spawning behavior. The seasonal variation developed for this study and described below was similar to the sine curve projection of the annual available prey cycle presented in fig. 5 of Jenkins (1979).

(1) July–February $P = 0.9$: this ration was required to reach 300 g by December 31; though prey abundance in winter is low, consumption requirements are also low.

(2) March–May $P = 0.4$: prey levels continue to decline, but consumption requirements increase markedly as temperatures warm to 18°C.

(3) June–July $P = 0.55$: the new year class of forage fishes becomes available, but are less than optimal size; consumption requirements are still increasing slightly.

(4) August–September $P = 0.7$: forage fishes are abundant and at optimal sizes; consumption requirements are still high.

Simulations were performed with different combinations of the variable components described above.

## Results

### Metabolic Rate Experiments

Change in metabolic rate as a function of temperature was similar for all three taxa (Fig. 2). No significant differences

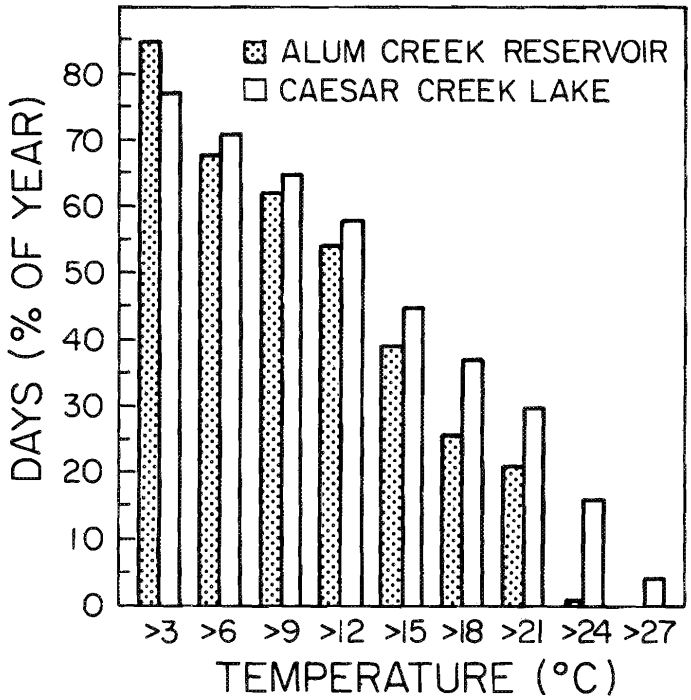



FIG. 1. Comparison of annual temperature regimes from the warm system (Caesar Creek Lake at 1 m) and the cool system (Alum Creek Lake at 6–7 m) that were used in the bioenergetics model.

($\alpha = 0.05$ unless noted otherwise) among taxa existed at 5 or 30°C, and no consistent pattern of significant differences occurred at the other temperatures (Table 2). These results indicate that the hypothesized differences between northern pike and muskellunge with regard to temperature were not evident for metabolic rate. Therefore, a single curve (eq. 1) for all three taxa was fit to all measurements of metabolic rate across temperature (Fig. 2):

$$M(\text{mgO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}) = (0.1025) \cdot (B^{-0.18}) \cdot (e^{0.055 \cdot T}).$$

The $a_2$ value becomes $9.27 \times 10^{-3}$ g·g$^{-1}$·d$^{-1}$ when used in the bioenergetics model. The $m$ value of 0.055 corresponds to a $Q_{10}$ of 1.73. The logarithmic transformation that was used to generate this curve introduced a bias (Beauchamp and Olson 1973) which can be corrected by multiplying the result by a correction factor of 1.075. Although we did not include this correction factor, this oversight should have little effect on the modelling results, because it affected all taxa equally.

## Food Consumption Experiments

Using an analysis of covariance procedure, we determined that there was a significant taxa–temperature interaction with regard to food consumption. To examine this interaction more closely, Duncan's multiple range test was used to document differences in mean consumption rates among taxa at each temperature (Table 2). At cool temperatures, 5 and 20°C, northern pike consumption was significantly greater than muskellunge (at 15°C the northern pike consumption was also greater than the muskellunge's, but not significantly so), and at warm temperatures, 27.5 and 30°C, muskellunge consumption was significantly greater than northern pike's. This supports the hypothesized difference between northern pike and muskellunge with regard to temperature. For the above reasons we chose to fit separate curves (eq. 3) to the food consumption data for each taxon (Fig. 3). These equations were included in the bioenergetics model to provide estimates of maximum food consumption rates at any temperature (Table 1). Caution should be taken when applying these equations to temperatures outside the range of our experimental temperatures (5–30°C). The optimum temperature for consumption can be calculated by differentiating equation 3 and finding the $T$ that provides a result of zero. These temperatures were 24.6, 26.7, and 23.5°C for northern pike, muskellunge, and tiger muskellunge respectively.

We also examined the differences in both conversion efficiency and growth among the three taxa (Table 2). The most noteworthy differences in conversion efficiency occurred at 5°C where northern pike were more efficient than muskellunge and the hybrid, and at 30°C where northern pike were less efficient than muskellunge or the hybrid. Generally, the most efficient temperatures for all three fishes were 20 and 22.5°C. Comparisons among means at different temperatures for each fish revealed that maximum efficiency occurred at a plateau across several temperatures. No differences existed among values from 20 to 27.5°C for both northern pike and muskellunge; conversion efficiency of the hybrid was highest between 15 and 22.5°C. The experimental method at 5°C (120-h starvation before weighing) may have resulted in conversion efficiency values lower than actual.

Differences in growth rates display trends that were similar to those found for food consumption and conversion efficiency. At 5°C northern pike grew faster than muskellunge or tiger muskellunge. Growth rates at 5°C for all three taxa may be lower than actual because of the methods used for 5°C. At 15°C the hybrid had greater growth than either of the parent species; hybrid growth was also fastest at 20 and 22.5°C, but not significantly so. By 25°C, growth rate of the hybrid had drastically decreased, so much so that hybrid growth was significantly slower than the parents' at both 25 and 27.5°C. As temperatures increased, the growth rate of the hybrid began decreasing at a cooler temperature than either parent. However, the decrease did not continue through 30°C as it did with northern pike, but leveled off such that hybrid growth rates were similar to those of muskellunge at 30°C, both significantly greater than the northern pike's.

## Predicted Versus Observed Growth Rate

To test the accuracy of the model derived from these experiments, simulations of the 2-wk food consumption experiments were run at the seven experimental temperatures with $P = 1.0$ to simulate ad libitum feeding. Starting weights for these simulations equalled the mean initial weight for each species at each temperature in experiments. Predicted growth rate was compared with the mean observed growth rate at each temperature for each taxon (Fig. 4). In all but two cases (northern pike and muskellunge at 5°C), predicted values were within one standard deviation of observed means. For all of the taxa, predicted values were neither consistently higher nor lower than observed values across temperature, suggesting that the 41% subtracted for SDA (14%), egestion (20%), and excretion (7%) was an acceptable approximation; however, accuracy of individual parameters could not be evaluated. For the same 2-wk simulations, the conversion efficiencies were slightly higher than those determined experimentally, which suggests that the actual values for $S$, $u$, and/or $f$ might be a little higher than our estimates.

When simulations were run with the same starting weight (20 g) for all fish at all temperatures and $P = 1.0$, optimal temperatures for growth were 24°C for northern pike, 26°C for

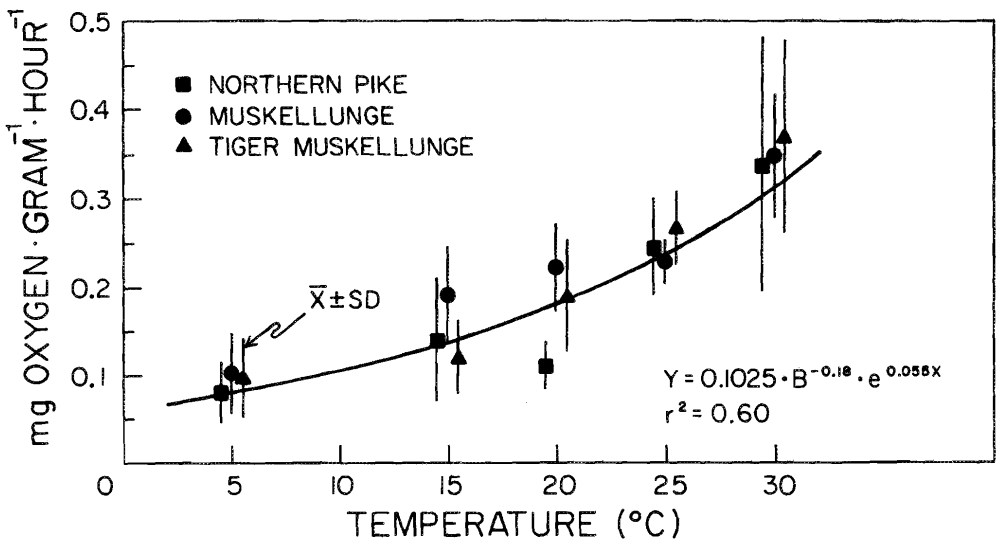



FIG. 2. Mean respiration rates (±1 SD) of northern pike, muskellunge, and tiger muskellunge determined at 5, 15, 20, 25, and 30°C in a closed static respirometer. A single exponential curve (dependent on temperature and weight) was fitted to all data.

TABLE 2. Mean metabolic rates, food consumption rates, gross conversion efficiencies, and relative growth rates at seven experimental temperatures positioned highest to lowest within each temperature. Species is denoted at the right of each value as NP (northern pike), M (muskellunge), or TM (tiger muskellunge). Values connected with vertical bars on the left side are not significantly different ($\alpha = 0.05$) as determined by Duncan's multiple range test (within temperature comparisons only).

| Test temperatures (°C) | | | | | | |
|---|---|---|---|---|---|---|
| 5 | 15 | 20 | 22.5 | 25 | 27.5 | 30 |
| *Metabolic rate (mg $O_2 \cdot g^{-1} \cdot h^{-1}$)* | | | | | | |
| 0.102 M | 0.191 M | 0.222 M | | 0.266 TM | | 0.371 TM |
| 0.097 TM | 0.140 NP | 0.190 TM | | 0.245 NP | | 0.349 M |
| 0.080 NP | 0.120 TM | 0.111 NP | | 0.228 M | | 0.339 NP |
| *Food consumption ($g \cdot g^{-1} \cdot d^{-1}$)* | | | | | | |
| 0.017 TM | 0.080 TM | 0.113 NP | 0.134 TM | 0.122 NP | 0.131 M | 0.127 M |
| 0.017 NP | 0.057 NP | 0.110 TM | 0.125 M | 0.119 M | 0.109 TM | 0.112 TM |
| 0.013 M | 0.052 M | 0.097 M | 0.103 NP | 0.098 TM | 0.108 NP | 0.082 NP |
| *Gross conversion efficiency (g growth·g consumed$^{-1}$)* | | | | | | |
| 0.261 NP | 0.337 TM | 0.368 TM | 0.377 TM | 0.357 M | 0.345 NP | 0.244 TM |
| 0.121 TM | 0.318 NP | 0.366 M | 0.377 NP | 0.345 NP | 0.366 M | 0.234 M |
| 0.117 M | 0.258 M | 0.355 NP | 0.359 M | 0.290 TM | 0.240 TM | 0.164 NP |
| *Relative growth ($g \cdot g^{-1} \cdot d^{-1}$)·100* | | | | | | |
| 0.44 NP | 2.67 TM | 4.09 TM | 5.12 TM | 4.36 NP | 4.40 M | 2.97 M |
| 0.21 TM | 1.85 NP | 4.01 NP | 4.49 M | 4.28 M | 3.81 NP | 2.74 TM |
| 0.17 M | 1.39 M | 3.49 M | 3.94 NP | 2.92 TM | 2.68 TM | 1.29 NP |

muskellunge, and 21°C for the hybrid. The optimal temperatures of northern pike and muskellunge were within their respective ranges of temperatures where maximum growth occurred in experiments, and the optimal temperature for the hybrid fell between the two temperatures where greatest growth occurred in experiments. When the same simulations were run with $P$ reduced to 40%, optimal temperatures for growth decreased about 3°C for all taxa. This follows the idea that optimal temperature for growth decreases as ration decreases (Kitchell et al. 1977).

## Bioenergetics Model Simulations

Even though we determined ration levels with the bioenergetics model using target weights from actual esocid field studies, the simulations (given available inputs) might not accurately predict changes in biomass experienced in the field. However, these simulations can predict differences among the three fishes and the importance of thermal regime, ration levels, and stocking date relative to these differences. The results of these simulations are found in Fig. 5; those simulations labeled

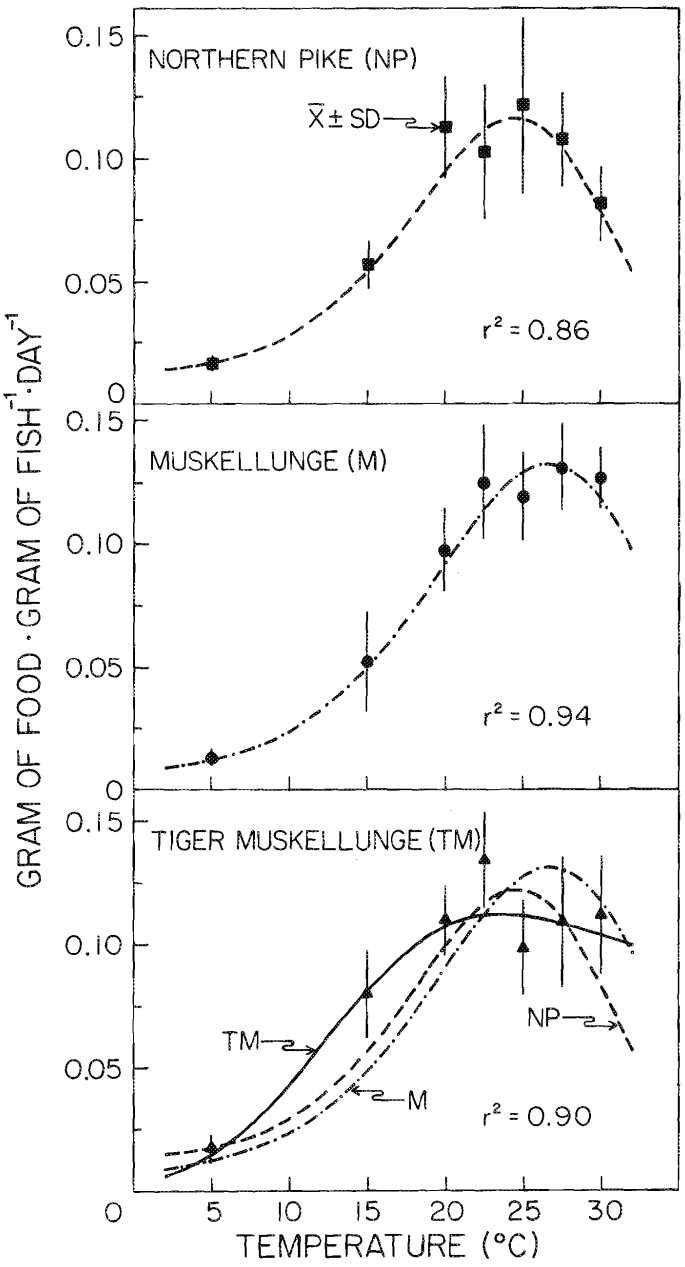



FIG. 3. Mean food consumption rates of northern pike, muskellunge, and tiger muskellunge determined in 2-wk laboratory experiments. Third-order polynomial curves were generated to fit these data; the bottom panel compares the curves of all three fishes.

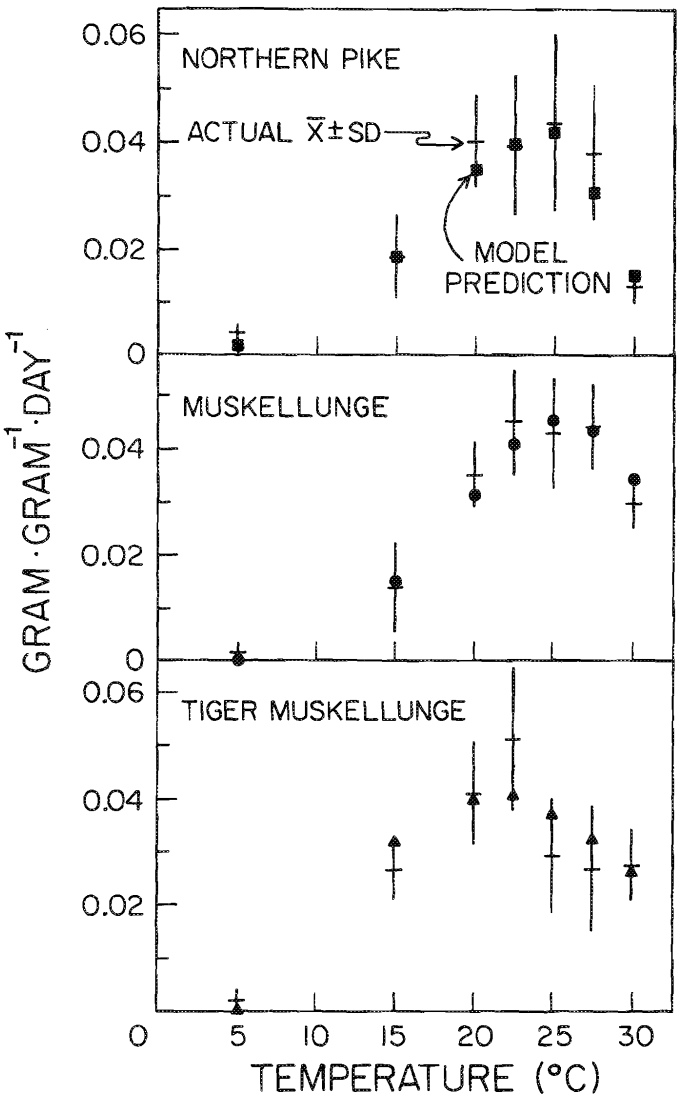



FIG. 4. Comparison of observed growth rates from 2-wk laboratory experiments and predicted growth rates (simulation of laboratory experiments) from a bioenergetics model for young-of-year esocids.

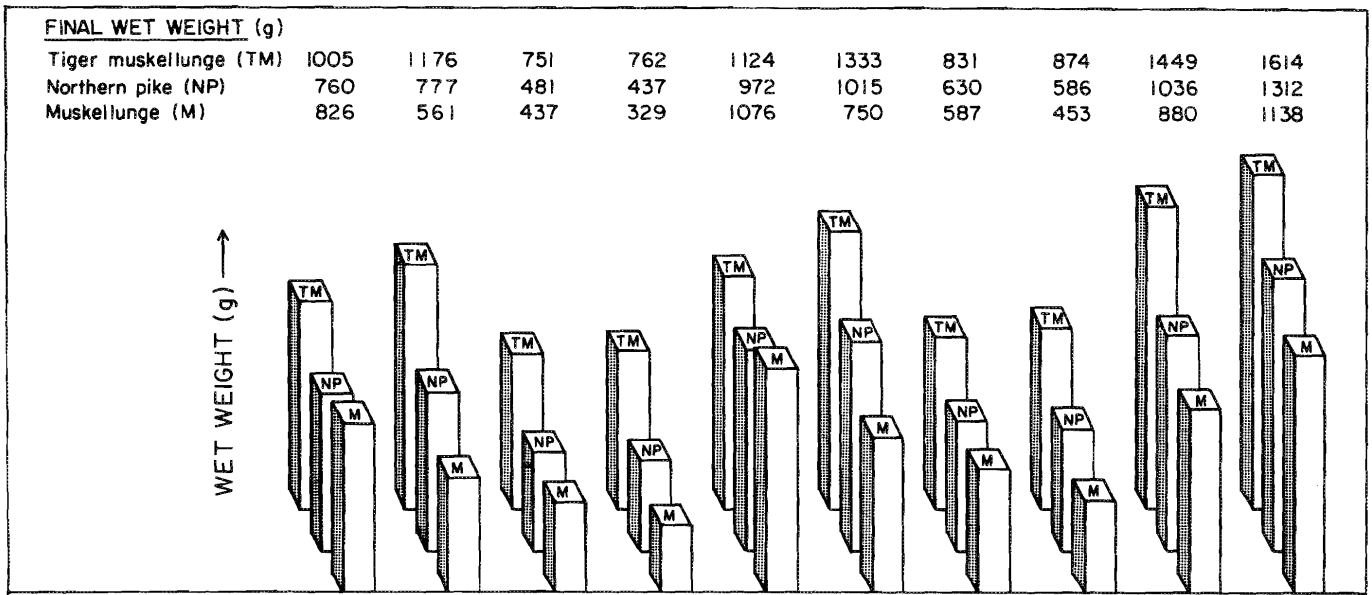
"C" differ from the "W" simulations only in that they were performed with the cool regime (C) instead of the more typical warm regime (W). Below, we examine two of these simulations in some detail.

*Simulation 1W*

In the warm thermal regime with constant ration, summer-stocked tiger muskellunge reached a greater final weight after 15 mo than either parent. Tiger muskellunge were 22 and 32% larger (by weight) than muskellunge and northern pike, respectively, and muskellunge were 9% larger than northern pike. (Note: percent weight differences were calculated as 100 × weight difference/weight of smaller fish.) These differences can be explained by examining the growth of these fishes throughout the simulation (Fig. 6, upper panel). During the first 3 mo following stocking (July, August, and September), warm temperatures (>20°C) allowed the muskellunge to grow fastest. As temperatures cooled from 20 to 10°C in October and November, muskellunge growth rates declined more rapidly than those of northern pike or tiger muskellunge, resulting in a weight advantage for the hybrid by the end of the first growing season. At this same time, cool temperatures allowed the northern pike weight to approach that of the muskellunge. Little or no growth occurred during winter. As temperatures warmed in spring, northern pike and hybrids began growing before muskellunge, and the hybrid increased its size advantage over its parents. However, warm temperatures in July and August temporarily slowed growth of northern pike and tiger muskellunge, resulting in a final ranking of sizes: tiger muskellunge > muskellunge > northern pike. The seasonal growth cycle that was produced by this simulation was typical of fish growth in temperate zones.

*Simulation 3W*

When the constant ration scheme (as in 1W) was replaced with a variable ration scheme in this simulation with the warm thermal regime and summer stocking, the final sizes of all taxa




| FINAL WET WEIGHT (g) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Tiger muskellunge (TM) | 1005 | 1176 | 751 | 762 | 1124 | 1333 | 831 | 874 | 1449 | 1614 |
| Northern pike (NP) | 760 | 777 | 481 | 437 | 972 | 1015 | 630 | 586 | 1036 | 1312 |
| Muskellunge (M) | 826 | 561 | 437 | 329 | 1076 | 750 | 587 | 453 | 880 | 1138 |

| SIMULATION | #1W | #1C | #2W | #2C | #3W | #3C | #4W | #4C | #5 | #6 |
|---|---|---|---|---|---|---|---|---|---|---|
| Thermal regime | | | | | | | | | | |
| Caesar Creek Lk. | X | - | X | - | X | - | X | - | - | - |
| Alum Creek Lk. | - | X | - | X | - | X | - | X | - | - |
| Thermoregulating | - | - | - | - | - | - | - | - | X | X |
| Stocking Date (wt.) | | | | | | | | | | |
| June 29 (9 g) | X | X | - | - | X | X | - | - | X | X |
| Sept. 27 (80 g) | - | - | X | X | - | - | X | X | - | - |
| Ration scheme | | | | | | | | | | |
| Constant | X | X | X | X | - | - | - | - | X | - |
| Variable | - | - | - | - | X | X | X | X | - | X |

FIG. 5. Different combinations of variable components (thermal regime (C = cool, W = warm), stocking date and weight, and ration) used in growth simulations of juvenile tiger muskellunge, northern pike, and muskellunge (lower panel), and the final weights (g) achieved with these simulations by September 27 of year following stocking (upper panel).

increased an average of 23%. Rank order of sizes remained the same, but relative differences between the hybrid and the smaller parent species decreased (tiger muskellunge and muskellunge weights were nearly the same, both about 14% greater than northern pike). The advantage that the hybrid had was reduced because the lowest ration (40% of $C_{max}$) occurred in spring when cool temperatures (10–20°C) most favored the hybrid.

Figure 6, lower panel, illustrates how the advantage in growth shifted from taxon to taxon depending on temperature and ration level. During the first 3 mo of the simulation (July–September), muskellunge grew faster because of the warmer temperatures. As temperatures declined in fall (October–November), the hybrid grew fast enough to surpass the parent species. Very little growth, if any, occurred during winter (December–February). When temperatures warmed in spring (March–May), the hybrid began growing soonest, but its growth was suppressed by low ration (40% of $C_{max}$). Growth rates increased noticeably when ration levels increased to 55% in June and July. Hot temperatures at the end of July caused a marked reduction in growth of northern pike and tiger muskellunge; at this point, muskellunge size surpassed that of northern pike and approached that of tiger muskellunge. High ration and high temperatures in late summer (August–September) allowed muskellunge to grow to nearly the size of tiger muskellunge and increase its small advantage over northern pike.

Under all conditions tested, tiger muskellunge grew fastest in every simulation. This supports claims of hybrid vigor even though it was not evident in the individual laboratory results. The hybrid growth advantage manifests itself due to combined effects of temperature and ration. In our simulations, thermal regimes alone favored tiger muskellunge because of prolonged periods of moderate temperatures (10–20°C) in spring and fall which were nearly optimal for their growth. Because more northerly lakes (extreme northern United States and Canada) have short warming and cooling periods (Diana 1982) and southern lakes have long periods during summer when temperatures are >25°C, thermal regimes of these systems might not favor the hybrid over its parents.

Northern pike grew faster than muskellunge except when summer stocking was coupled with the warm thermal regime. In this simulation, high temperatures during summer were less favorable to northern pike. These results, like those from laboratory experiments, support the hypothesis that northern pike should do better than muskellunge at cool temperatures and less well at warm temperatures.

Tiger muskellunge grew faster with the cool thermal regime than in corresponding simulations with the warm regime. Muskellunge always grew better in the warm system. Northern pike grew better in the cool system when stocked in summer, but better in the warm system when stocked in fall. Simulated thermoregulation increased growth in all three taxa. Mus-

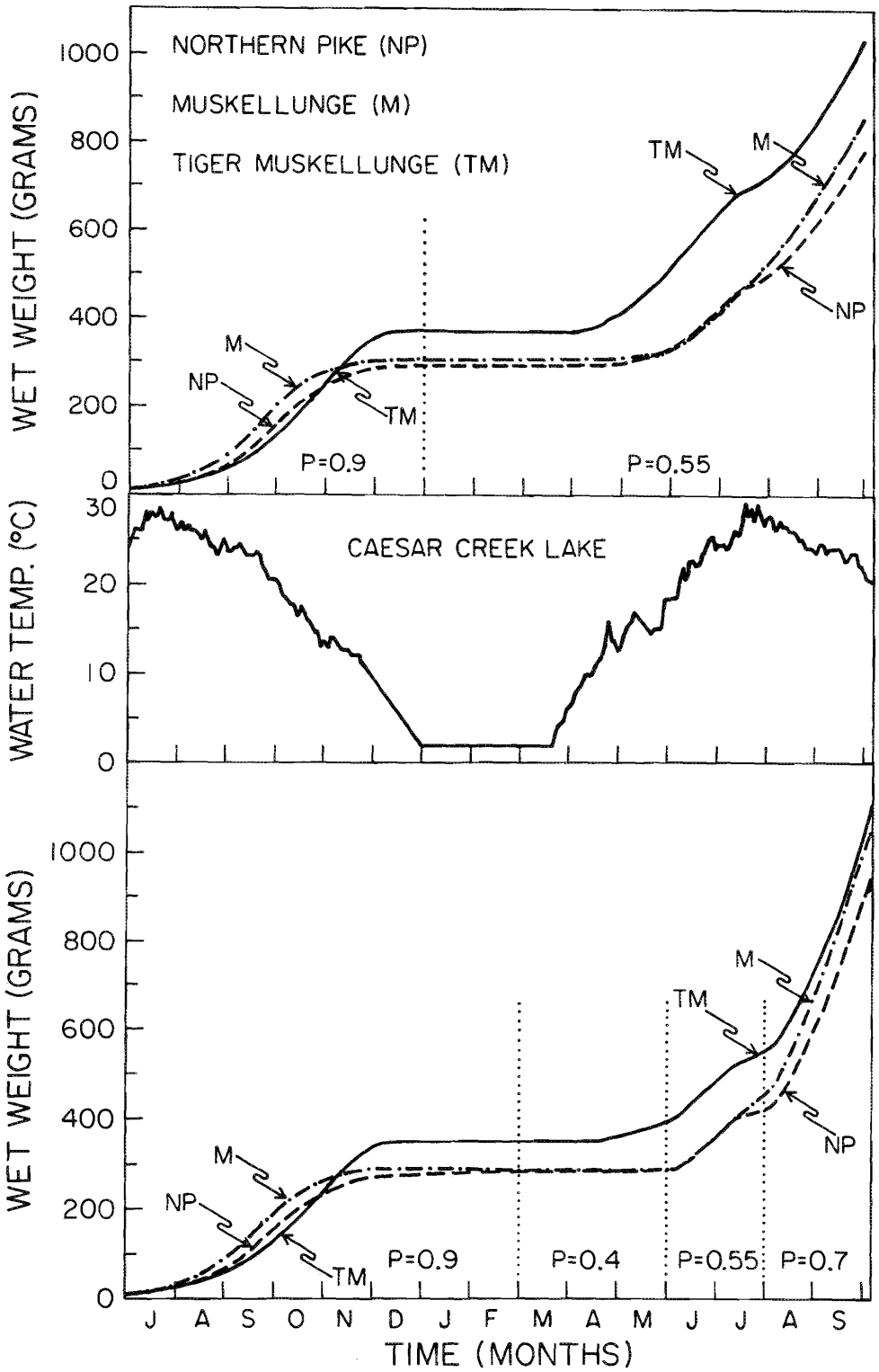



FIG. 6. Computer-simulated growth of summer-stocked esocids in a warm regime exposed to the constant ration scheme shown in the top panel (simulation 1W) and the variable ration scheme shown in the bottom panel (simulation 3W).

kellunge benefitted least from thermoregulation, because its thermoregulation temperatures differed least from lake temperatures. In systems with a shallow oxygenated epilimnion, where the benefits of thermoregulation would be limited, the advantage of tiger muskellunge would be reduced. As available epilimnetic temperatures increased, tiger muskellunge would be forced to spend time at temperatures farther from their optimal temperature (21°C) than either northern pike (24°C) or muskellunge (26°C).

With other conditions held constant (compare simulations 1 and 3 with 2 and 4, respectively), fish stocked in summer grew to a larger size than those stocked in fall, apparently because the

fish can grow faster in the field than in hatcheries during the 3 mo between summer and fall stocking dates. This could be due to a greater availability of forage and/or optimal temperatures in the field.

Best growth for all taxa was obtained when the prey base varied seasonally such that forage was most available during times when lake temperatures were most favorable for growth (compare simulations 1 and 2 with 3 and 4, respectively). However, as ration was varied seasonally, optimal temperatures sometimes did not coincide with high ration levels. For example, in May of simulation 3W (Fig. 6) when cool temperatures favored growth of tiger muskellunge, ration was only 40% of $C_{max}$; hence, tiger muskellunge grew slowly. In this same simulation, when hybrid growth was least favored by warm temperatures (August), ration was high, 70% of $C_{max}$. These conditions reduced differences in final sizes among the three taxa compared with differences when ration was constant (simulation 1W). In turn, if ration was overestimated in spring or underestimated in summer, hybrid advantage could possibly disappear.

## Discussion

Maximum growth of northern pike occurred at 25°C (24°C in simulations), which is 6° higher than the optimum temperature (19°C) that Casselman (1978) found within a Canadian stock of northern pike. Casselman also found that growth ceased at 28°C and that 29.4°C was the upper incipient lethal temperature. However, in our study, northern pike at 30°C were still growing. This suggests that local stocks might have adapted to the warm temperature regimes of Ohio waters during the 25 yr they have been maintained in Ohio hatchery ponds. Maximum growth and conversion efficiency of tiger muskellunge occurred at 22.5°C. Meade et al. (1983) found nearly the same results (maximum growth and efficiency at 23°C) for juvenile tiger muskellunge (120–130 mm) from parental stocks of a similar latitude (Pennsylvania) to Ohio. Our conversion efficiencies across the middle range of temperatures (15–25°C) for all three taxa ranged from 25 to 38%. These values compare favorably with those reported by Diana (1983) for YOY northern pike (42%; simulated), Johnson (1966) for YOY northern pike (30%; actual), Gammon (1963) for YOY muskellunge (37%; actual), and Brett and Groves (1979) for a typical young carnivorous fish (29%; averaged from actual data).

Since our study was completed, Diana (1983) also has published an energy budget for northern pike. Some notable differences exist between our study and his regarding the determination of parameters. Diana (1983) determined respiration rates for a larger size range of fish (5–1900 g versus 9–53 g), but at just two temperatures (compared with five in our work) and with a smaller sample size. The larger size range enabled Diana (1983) to develop a weight-dependent coefficient ($b_2$) which was also used in our study. Because Diana (1983) used only two temperatures, his temperature-dependent coefficient ($m = 0.16$) has a high potential for error; data at a third temperature might substantially modify his value for $m$. Diana's $m$ value translates to a $Q_{10}$ of 5.0. Brett and Groves (1979) suggested a general $Q_{10}$ of 2.3, and our $Q_{10}$ was 1.7. Though statistical comparisons of values from these two studies are difficult because of differences in fish sizes, the actual data points do not appear as different as do the values of $a^2$ (0.1025 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ (our study), 0.021 mg $O_2 \cdot g^{-1} \cdot h^{-1}$ (Diana 1983)), and $m$ (0.055 (our study), 0.16 (Diana 1983)) in their respective respiration curves.

Dolinin (1973) investigated the respiration of a Russian population of northern pike across temperature. A comparison of the oxygen consumption (mg $O_2 \cdot g^{-1} \cdot h^{-1}$) for a 600-g (approximate mean size used by Dolinin) northern pike determined experimentally (Dolinin 1973) and by equation (our study and Diana 1983) follows:

| Temperature (°C) | Dolinin (1973) | Our study | Diana (1983) |
|---|---|---|---|
| 5 | 0.020 | 0.043 | 0.015 |
| 10 | 0.040 | 0.056 | 0.033 |
| 15 | 0.070 | 0.074 | 0.073 |
| 20 | 0.107 | 0.097 | 0.163 |
| 25 | — | 0.128 | 0.363 |

Dolinin's (1973) observed data lie intermediate between the two sets of predicted values. Because metabolic rates are so low at ≤5°C, these differences are probably not as important as those at ≥20°C. The differences among these studies might be due to something other than experimental differences; the different geographical locations and thermal history of separate populations of fish might cause the fish to react differently across a range of temperatures.

Diana (1983) also determined factors for excretion, egestion, and SDA. However, he was not able to obtain a balanced budget with these values, so we chose to use the general values presented in Brett and Groves (1979).

How important are the simulated size differences among the three esocids? Some evidence suggests that the esocid that grows fastest as a juvenile will not necessarily grow fastest as an adult (Hess 1981). This observation might cancel any advantage fast-growing juveniles might possess. However, size differences among taxa after both the first and second growing seasons (nearly 90% in weight in some simulations) should be large enough to influence survival. Large fish are less susceptible to natural mortality (Kipling and Frost 1970) and predation (Stein et al. 1981) and have wider diet range with respect to prey size than small fish (Gillen et al. 1981). Wide diet ranges might enhance survival during periods when preferred sizes of prey are scarce, as in winter or spring. These factors probably influence survival more strongly when fish are young; therefore, growth during the first year of life might be most critical to long-term survival.

However, growth and final size at the end of 12–15 mo are not the only considerations in generating appropriate stocking policy. Small esocids stocked in summer may be susceptible to intense predation by largemouth bass at stocking (Stein et al. 1981); only stocked hybrids greater than 250 mm (the large size in the simulations) are invulnerable to these predators. Consequently, managers must weigh the benefits of the eventual large size of summer-stocked fish against the higher short-term survival of fall-stocked fish. Clearly, if few summer-stocked fish survive, long-term growth differential becomes unimportant. Also, when stocking different sizes of fish during different seasons, the match between predator size and prey size becomes important. Small fishes with narrow diet ranges may be less likely to grow as well as their large counterparts, which are able to consume a wide range of prey (Gillen et al. 1981). Thus, the bioenergetics model should be used in conjunction with information on predator–prey size ratios, vulnerability to resident predators, and other factors not incorporated into this approach.

Another factor to weigh when considering various stocking strategies is the apparent adaptability of northern pike to the

warm waters encountered in Ohio reservoirs. This plasticity in northern pike which allows them to adapt to warm environments, given the necessary time to do so, could be an important consideration in continuing efforts to stock non-native fishes. If such plasticity is inherent in other fishes, it should be considered when deciding where to obtain fish for stocking, i.e. from a particular race or subspecies, or from a particular geographic region or latitude. For example, if a coolwater species is being stocked in a region where warm summer temperatures may affect survival, then brood stock should be selected from a population that is as southern as possible. Given the adaptability of these fish and their apparent difference from Canadian stocks, caution should be taken in extending the results of this study to populations of esocids outside the midwestern United States.

Bioenergetic models can aid management decision-making and suggest areas for further field research. In this case, the large differences in final weights between simulations with variable ration and those with constant ration suggest that accurate estimation of ration is necessary to estimate growth. The ration values we used were only rough estimates based on prey abundances. More accurate data on seasonal ration levels and their relationship to prey abundance and availability are needed, especially for young fish. Another important quality of the model is its flexibility. For example, given changes in mean weight through time, rate of food consumption can be determined; Cochran and Rice (1982) estimated largemouth bass food consumption over a 4-mo period using mean weights measured on nine sampling dates. If quantitative estimates of prey populations are coupled with this analysis, correlations of prey availability with actual consumption could be formulated, thereby enabling one to predict consumption rates based on prey availability data and vice versa. If initial population size and mortality rates are included in the model, the quantity of forage necessary to support a population or to achieve a desirable size of predator can be determined (Stewart et al. 1981). In this form the model also can predict the predatory effect on a prey population. With historical knowledge of year-to-year fluctuations in the prey base, a maximum level of predation can be defined based on minimum population levels of the prey, thus providing useful information for determining maximum stocking densities of predators.

The model could also be applied to estimate the uptake and accumulation of pollutants (e.g. heavy metals, radioisotopes, and pesticides). This type of modelling has already been done with northern pike (Carlsson 1978; Fagerstrom and Asell 1973; Fagerstrom et al. 1974), but these models were developed with little actual northern pike data. The temperature-related and weight-related data presented here and in Diana (1983) should be very useful for this type of modelling in the future.

In summary, the experimental data suggest that the physiological differences between the parent species with regard to temperature are related to the latitudinal differences in their natural geographic distributions, and that the hybrid is not particularly similar to either parent. The Ohio stock of northern pike, whose brood stock is maintained in hatchery ponds, has apparently adapted to warm Ohio waters. If this apparent adaptation had not occurred, a larger difference between the northern pike and muskellunge might be expected. Based on bioenergetic considerations, tiger muskellunge outgrew both northern pike and muskellunge in a thermal regime common to Ohio waters and in a cooler thermal regime, which was atypical of Ohio systems. In systems with few predators and an abundant prey base of soft-rayed fishes, this hybrid should outgrow and perhaps survive better than its parents. Comparative work that better defines the role of resident predators and forage base on the survival and growth of all three taxa is required before definitive taxon-specific stocking recommendations can be made.

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